THE WINGS OF INSECTS.

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CHAPTER IV (*Concluded*).

The Specialization of Wings by Addition.

V. THE TRACHEATION OF THE WINGS OF ORTHOPTERA.

THE study of the tracheation of wings of orthopterous nymphs was undertaken merely for the purpose of determining the homologies of the wing-veins in this order; but some of the results attained have a much wider bearing, giving a hint as to the position of this order in the class Insecta. For this reason, after setting forth the conclusions regarding the homologies of the tracheæ of the wings, a brief discussion of the taxonomic bearing of some of these conclusions will be given.

The Homologies of the Principal Tracheæ of the Wings of Orthoptera. — In this investigation representatives of the Blattidæ, Acrididæ, Locustidæ, and Gryllidæ have been examined; no living nymphs of members of the Mantidæ nor of winged Phasmidæ were studied. It is not probable, however, that these will present serious difficulties.

The most uniform characteristic of the wings of the four families studied is the structure of the anal area of the hind wings. For this reason we will begin our description of the tracheation of the wings with this area and proceed cephalad.

In the Orthoptera the anal area of the hind wings is broadly expanded and fanlike in form. The first anal trachea is simple (Figs. 74–78 *A*); the second and third anal tracheæ coalesce for a distance and then separate into several tracheæ, each of which traverses a convex vein of the fanlike portion of the wing. Sometimes, as in the wing of an Acridid, represented by Fig. 75, the common trunk of these two tracheæ divides into two large trunks, which probably correspond to the second and third anal tracheæ respectively; but in most cases this division is not clearly indicated.

In many of the saltatorial Orthoptera the anal area of the hind wings bears a striking resemblance to the wings of Ephemerids, there being a regular alternation of convex and concave veins. In these cases the concave veins are evidently a later development than the convex veins. The increase in the number of the branches of the anal tracheæ takes place at the caudal end of the series, and about each added trachea a convex vein is developed. It is only after the space between two of these convex veins becomes wide enough to admit of a fold in the wing that a concave vein is developed, and this development takes place in the same manner as in the Ephemerida. In some cases, as in the hind wings of Scudderia (Fig. 77), a tertiary set of anal veins is developed; these extend only a short distance from the margin of the wing, and increase the resemblance of this area to an Ephemerid wing.

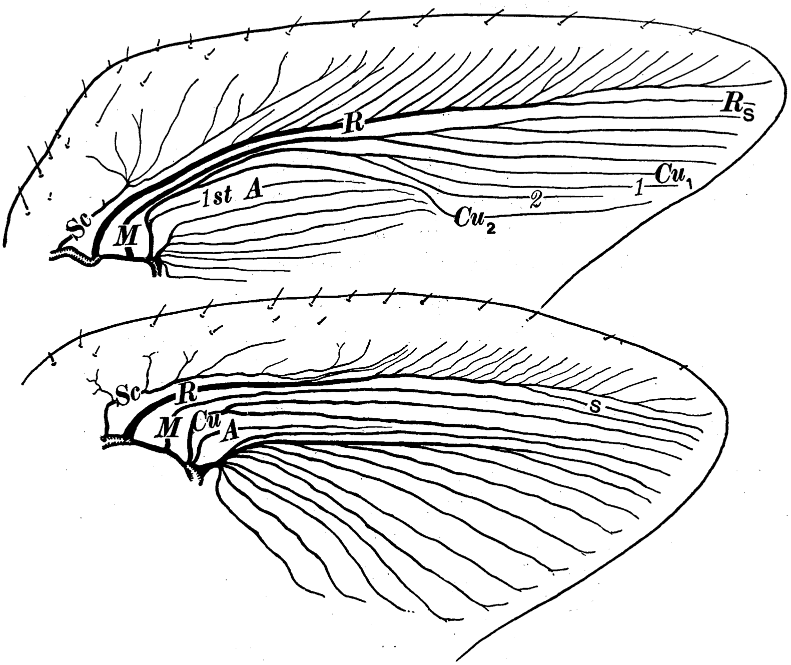

Fig. 74. — Wings of a nymph of a cockroach.

The cubital trachea of the hind wings varies greatly in form, even within the limits of a single family. In the Acrididæ it is sometimes reduced to an unbranched condition (Fig. 75 *Cu*); in all of the Locustidæ known to us it retains the primitive two-branched condition (Fig. 76); in Œcanthus (Fig. 78) there is a single accessory cubital trachea; while in certain cockroaches, not figured here, vein Cu_1 is pectinately branched.

Similar variations in the number of branches of each of the other principal tracheæ of the hind wings occur. It is not necessary to point them out in detail, as they are sufficiently indicated by the lettering of the figures. The most striking features are the reduction of the radius, the radial sector being at most unimportant, and in some cases entirely wanting, and the loss of the costal trachea.

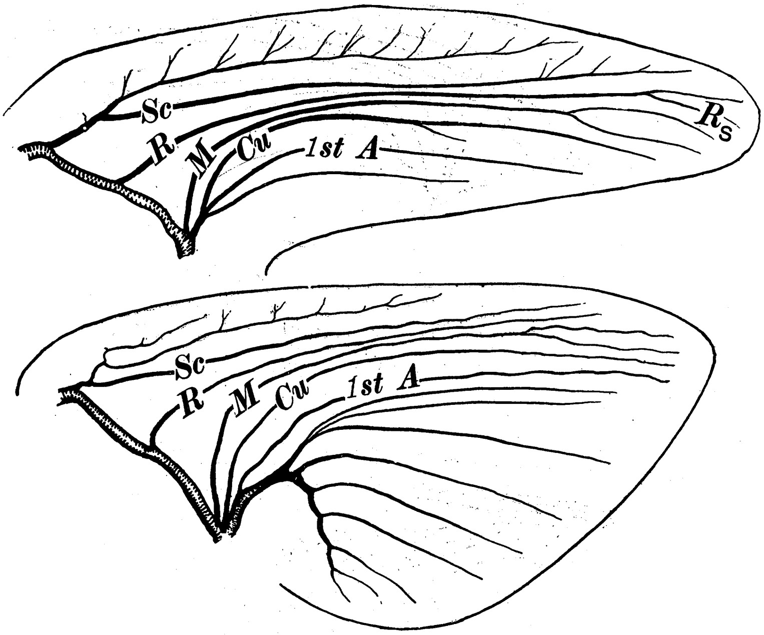

FIG. 75. — Wings of an Acridid nymph.

In the fore wings the anal area is variously modified in the different members of the order. In the female Œcanthus (Fig. 78) it nearly retains its primitive form; in the Acridid, represented by Fig. 75, a reduction of this area has taken place; while in the Blattidæ (Fig. 74) the three anal tracheæ are pre-

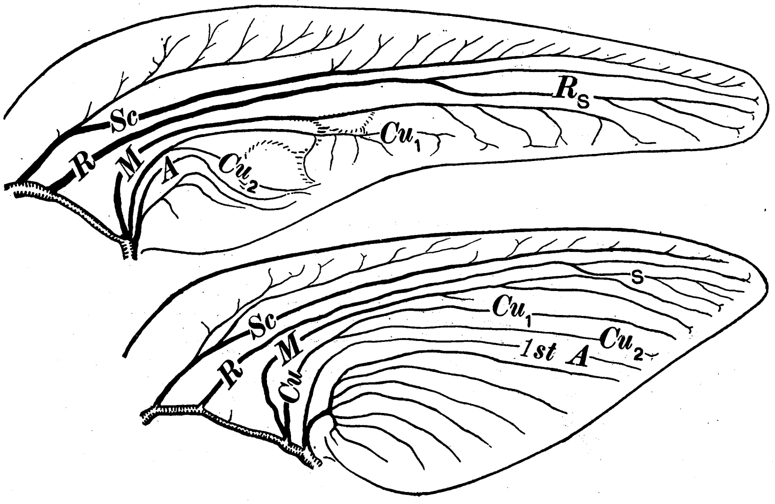

FIG. 76. — Wings of a nymph of Conocephalus.

served and the second and third have been specialized by addition, these tracheæ consisting of several parallel branches.

The cubital trachea is reduced to a nearly simple condition

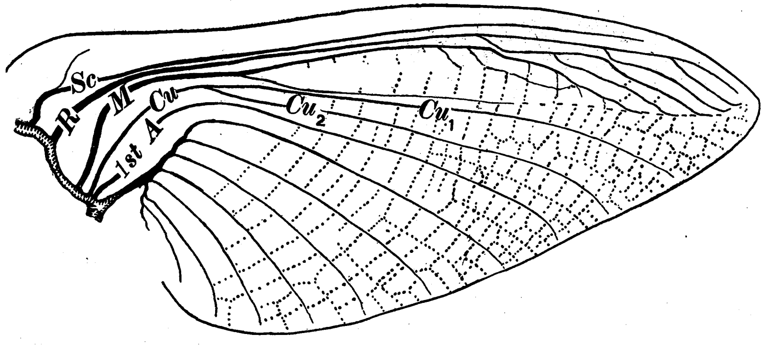

FIG. 77. — Hind wing of a nymph of Scudderia. Dotted lines indicate adult venation in part.

in the Acridid (Fig. 75); but in the other forms examined accessory tracheæ are developed on the caudal side of trachea *Cu*1.

In the males of the Locustidæ (Fig. 76) and of the Gryllidæ (Fig. 79) the formation of a musical organ has been attained by a modification of the cubital and anal areas. An extreme case of this is furnished by the male Œcanthus (Fig. 79). The principal vibrating area of the wing lies between the branches of the cubitus, which diverge widely in this sex.

A study of the musical organs of adult Orthoptera throws light on the nature of the anal furrow. In the female this furrow lies between the cubitus and the first anal vein; but in the males of the Locustidæ and Gryllidæ the anal furrow crosses vein Cu_2. It is evident, therefore, that this furrow is merely a fold in the adult wing, and that its position is variable. It has already been shown[1] that in the Heteroptera, when an anal furrow is developed, it is in front of the cubitus, instead of in the more usual position between the cubitus and the first anal vein.

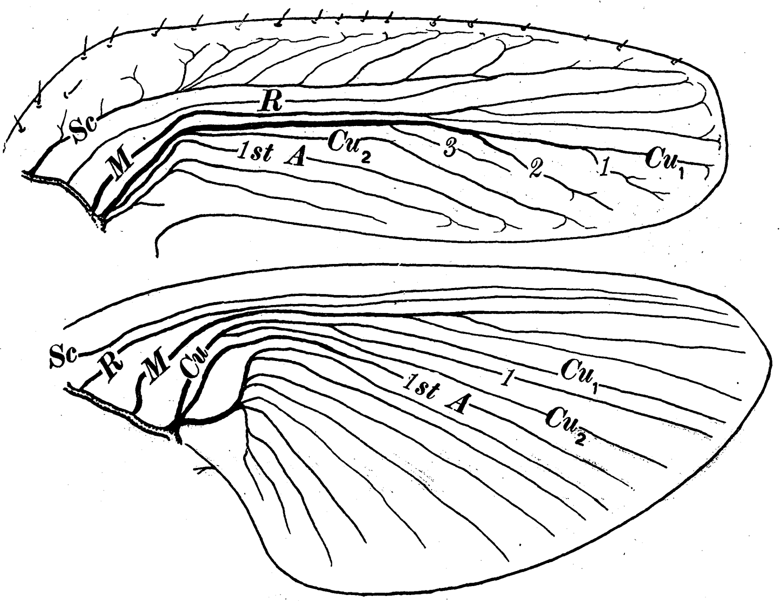

Fig. 78. — Wings of a female nymph of Œcanthus.

Although the wings of the two sexes of Œcanthus present a very different appearance, there is really a very close correspondence in the tracheation (and consequently in the venation) of the two, as can be seen by comparing the lettering of Figs. 78, 79; the same number of anal veins and of accessory cubital veins exist in the two sexes.

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[1] *American Naturalist*, vol. xxxii, p. 252.

The lettering of the figures will serve to show the striking differences in the development of the remaining veins in different members of the order. Thus, for example, while the radius is the most prominent vein in the fore wing of the cockroach (Fig. 74), in Œcanthus (Figs. 78, 79) it is the least developed of the principal veins; or, to take another example, the subcosta is greatly reduced in the cockroach (Fig. 74), while in the Acridid (Fig. 75) and in the Locustid (Fig. 76) it is as well developed as any other vein.

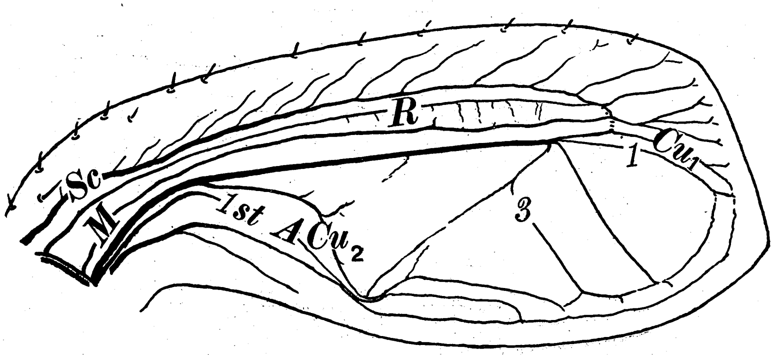

FIG. 79. — Fore wing of a male nymph of Œcanthus.

In none of the Orthoptera that we have examined is the costal trachea distinctly preserved. Frequently, as in the Acridid (Fig. 75) and in the Locustid (Fig. 76), there is a prominent branch of the subcostal trachea which simulates a costal trachea; but that this is merely an overgrown branch of the subcostal trachea is evident when a series of forms are studied; in the hind wing of Conocephalus (Fig. 76) there are two such branches.

It will be remembered that in our hypothetical type the subcosta is two-branched, and that the branches are designated as *Sc*1 and *Sc*2 respectively. A good example of this typical branching of the subcosta is afforded by Nemoura.[1] But there are no indications that the primitive branching has been retained in the Orthoptera; here, when the two-branched condition exists, it is a secondary development; it would be misleading, therefore, to designate these branches as Sc_1 and Sc_2, for they do not correspond to the branches so designated in other orders. In this case the branch, or branches, of the subcostal trachea are merely accessory branches, like the accessory branches developed on other principal tracheæ.

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[1] *American Naturalist*, vol. xxxii, p. 238, Fig. 8.

Although the costal trachea has been lost, the thickening of the costal margin of the wing should be called the costal vein; for it is still the vein that was formed about the costal trachea in the beginning.

The few illustrations given here will show how easily the homologies of the tracheæ of the wings of orthopterous nymphs, and consequently of the veins that are formed about them, can be determined. But if one studies only the wings of adults, where many cross-veins have been developed, and where the basal connections of the principal veins are obscured, it is extremely difficult to determine these homologies. It is also evident that the wings of these insects present many characters which are easily available for taxonomic purposes.

The Position of the Orthoptera in the Class Insecta as indicated by the Tracheation of the Wings. — The making of genealogical trees does not fall within the scope of the present series of papers. Our object has been to learn in what ways wings have been modified in order to determine the homologies of the wing-veins. It is obvious that this had to be done before the characters presented by the wings could be used intelligently in working out the phylogeny of the orders. Now that this has been accomplished, it would be possible to propose a provisional classification of insects based on the characters of the wings; but we feel that it is much better to wait till the results we have attained can be correlated with similar studies of other organs. There is, however, one character in the tracheation of the wings to which it seems worth while to call attention now.

In most insects the principal tracheæ of the wings form two quite distinct groups. These we have already designated as the costo-radial and the cubito-anal groups respectively.[1] To the former belong the costa, the subcosta, and the radius; to the latter, the cubitus and the anal veins. These groups find their attachment to the main tracheal system of the body at points wide apart; in the Perlid genus, Capnia, the former group springs from the dorsal lateral trunk, the latter from ventral lateral trunk of the thorax.[2] Even in such groups as Trichoptera, Hymenoptera, and Diptera, where great reduction has taken place, the persisting tracheæ clearly represent these two groups.

The media is sometimes a member of the costo-radial group (Fig. 80) and sometimes of the cubito-anal group (Fig. 76). In certain forms, however, the media arises midway between these two groups from a transverse basal trachea which joins them, suggesting at once the possibility of its migration from one group to the other. Since there is no evidence of its having entered the wing independently, to which of the two groups did it belong in the primitive winged insect? The answer lies (1) in the rank of the insects showing the different conditions, and (2) in the ontogeny of the media itself.

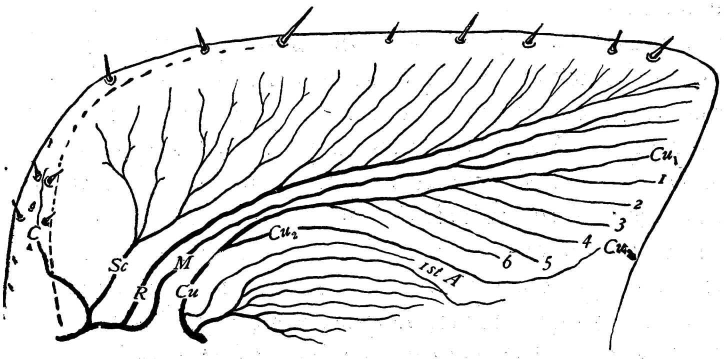

FIG. 80. — Fore wing of a nymph of a cockroach.

(1) Only in the Plecoptera and in some of the Blattidæ does the media clearly belong to the costo-radial group, and in these there is no basal transverse trachea connecting the two groups;

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[1] *American Naturalist*, vol. xxxii, p. 88.

[2] A fact of no little interest in its relation to the question of a former respiratory function in these or closely related parts; since tracheal gills are commonly joined to both longitudinal lateral trunks, securing, doubtless, better distribution of the air.

in all other insects we have studied, the two groups are connected and the media is either joined to the cubito-anal group or arises from the transverse basal trachea. No one will hesitate to believe that the Plecoptera and the Blattidæ are the ones more likely to have retained the more primitive structure.

(2) We have previously shown[1] that in a Cicada nymph one-third grown the medial trachea springs from the transverse basal trachea midway between the radial and the cubital tracheæ, while in the grown nymph it has reached the cubital trachea. In most insects of which we have had nymphs of various ages we have observed the same direction of migration; never any migration in the opposite direction.

From this it follows that, in arranging the orders of winged insects in an ascending series, if we take into account only the structure of the wings, the Plecoptera should be placed first; for this order, as a whole, retains the primitive condition of the basal connections of the wing tracheæ. Next to this in degree of divergence from the primitive wing type stand the Orthoptera, with the Blattidæ the lowest of the series of orthopterous families; for in this family alone is the primitive condition of the basal connections of the wing tracheæ retained.

In this connection attention should be called to the striking similarity of the anal area of the hind wings in the Orthoptera and in the Plecoptera; in both cases the fanlike portion is supported by the second and third anal veins, while the first anal vein remains simple.

An understanding of the nature of the changes that are taking place in the basal connections of the wing tracheæ renders this region of the wing a very instructive one. Let us examine again the figures herewith given: In the wing of a cockroach, represented by Fig. 80, the primitive type is retained, the medial trachea is a member of the costo-radial group, and there is no transverse basal trachea; while in the wings represented by Fig. 74 the basal trachea is well developed, and the medial trachea has begun its migration toward the cubito-anal group, but it still arises from the basal trachea. In all other forms here figured the base of the medial trachea has nearly or quite reached the cubital trachea and usually coalesces to a greater or less extent with it. An extreme case of this migration is illustrated by Xiphidium (Fig. 81). And here there appears to be a reduction of the transverse basal trachea. It has served its purpose, and, like an abandoned road, is disappearing from view. It will not be surprising if Locustid nymphs are found in which this connection between the two groups is lost, but the presence of the medial trachea in the cubito-anal group will show it to have existed.

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[1] *American Naturalist*, vol. xxxii, p. 249.

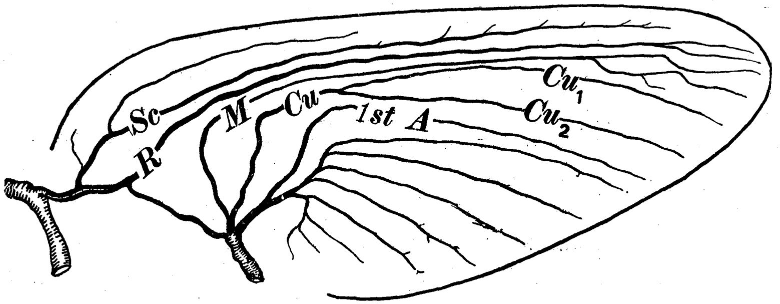

FIG. 81.— Hind wing of a nymph of Xiphidium.

In the Acridid, represented by Fig. 75, the radial trachea is following the medial in its migration; this is indicated well by the curve near the base of the radial trachea in the hind wing.

VI. CONCLUSION OF CHAPTER IV.

In this and the preceding chapter we have furnished data for determining the homologies of the veins in each of the orders of winged insects except the Euplexoptera, Mecaptera, Isoptera, and the Physopoda. Of the first two we have been unable to procure immature stages; it is not probable, however, that they will present serious difficulties when they are studied. Of the Isoptera we have examined nymphs of two genera, Termes and Termopsis, but we wish to examine other forms before publishing conclusions. In all of the Physopoda that we have seen, the tracheation of the wings is so reduced that we have been unable to determine definitely the homologies of the few remaining tracheæ. We therefore close at this point our discussion of this phase of the subject and pass to a study of the beginning of wings.